

The Effect of Visual Experience on the Development of Functional Architecture in hMT+

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We investigated whether the visual hMT+ cortex plays a role in supramodal representation of sensory flow, not mediated by visual mental imagery. We used functional magnetic resonance imaging to measure neural activity in sighted and congenitally blind individuals during passive perception of optic and tactile flows. Visual motion-responsive cortex, including hMT+, was identified in the lateral occipital and inferior temporal cortices of the sighted subjects by response to optic flow. Tactile flow perception in sighted subjects activated the more anterior part of these cortical regions but deactivated the more posterior part. By contrast, perception of tactile flow in blind subjects activated the full extent, including the more posterior part. These results demonstrate that activation of hMT+ and surrounding cortex by tactile flow is not mediated by visual mental imagery and that the functional organization of hMT+ can develop to subserve tactile flow perception in the absence of any visual experience. Moreover, visual experience leads to a segregation of the motion-responsive occipitotemporal cortex into an anterior subregion involved in the representation of both optic and tactile flows and a posterior subregion that processes optic flow only.

Keywords: blind subjects, functional magnetic resonance imaging (fMRI), hMT+, optic flow, supramodality, tactile flow

Introduction

Coherent changes in visual images caused by object or viewer movement are called "optic flow" (Gibson 1950). Optic flow provides information about object form, position, orientation, and movement, as well as information about motion of the self within the environment (Gibson 1950, 1958). Correct attribution of optic flow to object movement or self-movement requires integration of visual and kinesthetic inputs. "Tactile flow" involves analogous changes in tactile images caused by object or subject movement. Tactile flow, like optic flow, gives information about object form, position, consistency, and movement, as well as information about the position and movement of one's own body or body parts. Visual and tactile representations of flow are merged into a unified percept of object and self-motion. Bicchi et al. (2003) have proposed that tactile flow can be modeled with the same equations that are used to model optic flow. For example, models of optic flow predict the aperture problem, or "barber pole illusion," and tactile perception of

slanted moving edges produces the same illusion. Concentric spread in optic flow conveys information about speed of approach; in tactile flow, an analogous concentric spread conveys information about softness (Bicchi et al. 2000).

Perception of visual motion activates the human extrastriate cortical region, middle temporal complex (hMT+) (Watson et al. 1993; Zeki et al. 1993; Tootell, Reppas, Dale, et al. 1995). This area also is activated during mental imagery of movement (Goebel et al. 1998), perception of flickering stimuli that induce apparent motion (Goebel et al. 1998; Muckli et al. 2002), and perception of stationary stimuli that induce illusory motion (Tootell, Reppas, Dale, et al. 1995; Tootell, Reppas, Kwong, et al. 1995; Goebel et al. 1998; Muckli et al. 2002) or imply movement (Kourtzi and Kanwisher 2000). Furthermore, subdivisions of hMT+, the middle temporal area (MT) and the medial superior temporal area (MST), respond selectively to different components of optic flow (Morrone et al. 2000; Huk and Heeger 2002; Huk et al. 2002). Translation evokes activity in a more posterior and superior location (MT) than does rotation (MST) (Morrone et al. 2000). These subdivisions also can be distinguished by their retinotopy and response to peripheral ipsilateral stimuli (Huk et al. 2002).

hMT+ also is activated during perception of tactile motion (Hagen et al. 2002; Blake et al. 2004), raising the question of whether this area is strictly visual or plays a more general role in the supramodal representation of sensory flow. Because mental imagery of visual movement also activates hMT+ (Goebel et al. 1998), however, activation during perception of tactile motion may be mediated by visual mental imagery.

Functional magnetic resonance imaging (fMRI) studies have shown that a region in the ventral extrastriate cortex, lateral occipital tactile-visual (LOtv), is activated by both visual and tactile perception of objects (Amedi et al. 2001; Pietrini et al. 2004). Visual and tactile object recognition evoke common category-specific patterns of neural activity in LOtv of sighted subjects (Pietrini et al. 2004). LOtv also is activated during tactile object recognition in congenitally blind individuals (Pietrini et al. 2004), demonstrating that the participation of this area is not mediated by visual imagery and that the development of this functional architecture does not require visual experience. Recent findings have demonstrated that the dorsal extrastriate and parieto-occipital cortical areas also are involved both in visual and tactile spatial discrimination tasks, thus

supporting a “supramodal” organization of the dorsal stream (Sathian et al. 1997; Prather et al. 2004; Reed et al. 2005; Ricciardi et al. 2006). Thus, the “visual” cortices in both the ventral and dorsal pathways can process information independently from the sensory modality that carries that information to the brain.

Given the supramodal representation of object form and spatial location in visual extrastriate cortex, we hypothesized that the representation of sensory flow in hMT+ may also be supramodal. The previous reports that showed that hMT+ is activated during tactile motion perception (Hagen et al. 2002; Blake et al. 2004) did not exclude the possibility that hMT+ activity during tactile motion perception is mediated by visual motion imagery (Goebel et al. 1998). We decided to investigate whether the activation of hMT+ during the perception of tactile movement reflects a supramodal representation of sensory flow or is simply mediated by visual imagery. To address this question, we measured neural activity, using fMRI, in sighted subjects and in subjects with congenital or early blindness. The study of blind subjects who have either had no visual experience or had no visual recollection allows one to test the role of visual imagery. Additionally, the study of these subjects allows one to investigate the role of visual experience in the development of the functional organization of sensory representations.

Materials and Methods

Subjects

Seven sighted (2 females, 27 ± 2 years) and 4 blind (1 female, 37 ± 14 years) healthy volunteers participated. All subjects were right handed. Three blind subjects were blind from birth, and one became blind at the age of 2 years and had no recollection of any visual experience (causes of blindness: 2 congenital glaucoma, retinopathy of prematurity, and congenital optic atrophy). All subjects received medical, neurological, and psychiatric examinations and a structural magnetic resonance imaging (MRI) brain scan to exclude any disorder other than blindness. No subject was taking any psychotropic medication. All subjects gave their written informed consent after the study procedures and risks were explained.

Image Acquisition

We used fMRI to measure brain activity while subjects perceived tactile and visual motion. Gradient echo echoplanar images were acquired with a GE Signa 1.5-T scanner (General Electric, Milwaukee, WI) (repetition time = 3000 ms, 22–26 axial slices, slice thickness = 5 mm, field of view = 24 cm, echo time = 40 ms, flip angle = 90° , and image plane resolution = 64×64 pixels). Voxels were $3.75 \times 3.75 \times 5$ mm. High-resolution T_1 -weighted spoiled gradient recall images were obtained for each subject to provide detailed brain anatomy.

We obtained 3–7 time series in each subject while they perceived tactile motion and 2–4 time series while they perceived visual motion. Each time series consisted of 79 brain volumes (237 s).

Tactile Motion Stimuli

Tactile stimuli were moving or static Braille-like dot patterns presented on a plastic flat surface (a 30-mm-wide band). We used 2 types of motion: horizontal translation (left to right and right to left) and rotation (clockwise and counterclockwise). Dots (average diameter: 1–1.5 mm; height: 0.5–1 mm; Fig. 1) were randomly distributed on the surfaces (translational: density 1 dot/cm², average distance: 9 mm; rotational: density 2 dot/cm², average distance: 6 mm), so not to recollect any letter of the Braille alphabet in blind individuals (the moving 2-point discrimination must be less than 4 mm for a Braille letter), and moved at about 2.2 cm/s translationally or 93.5°/s rotationally. We presented tactile stimuli using an MRI compatible device (Fig. 1) on a polystyrene table placed over the subjects' legs. Subjects' hands lay on the table with the index and middle fingers touching the plastic surface with dot patterns. Type of movement, direction of movement, and side of stimula-

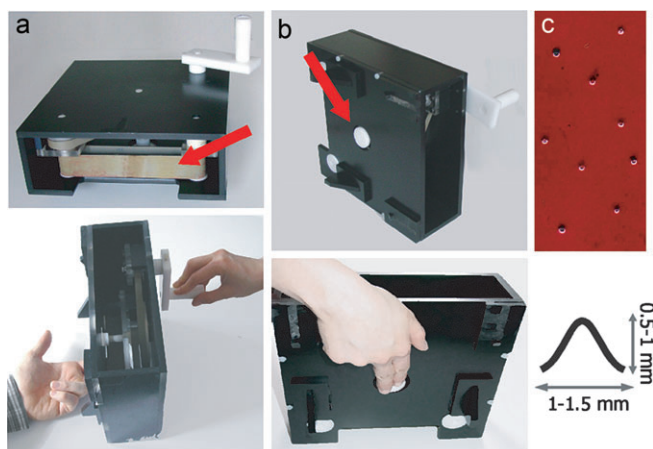


Figure 1. A magnetic compatible device (placed on a polystyrene table over the subjects' legs) moved Braille-like dot patterns on a plastic surface to provide translational (a) and rotational (b) tactile flow stimulation. Subjects' hands lay on the table with the index and middle fingers touching the plastic surface with dot patterns. (c) A particular of the 30-mm-wide band with random Braille-like dot patterns and a graphic representation of a tactile dot are shown.

tion (right hand or left hand) were randomized and counterbalanced within and across subjects.

Visual Motion Stimuli

Visual stimuli were moving or static white dots presented on a black background (dot radius: 0.06° , luminance about 20 cd/m²). We used the same 2 types of motion as we used for tactile motion: horizontal translation (50 dots moving left to right and right to left at 1.8°/s) and rotation (50 dots moving clockwise and counterclockwise at 9°/s). Visual stimuli were presented on a rear projection screen viewed through a mirror (visual field: 25° wide and 20° high). A central static white cross provided a fixation point ($0.15^\circ \times 0.15^\circ$). Participants were asked to fixate the central white cross.

Task

We presented moving stimuli in 8- to 40-s blocks separated by intervals with static stimuli of varying duration (11 ± 10 s). Each time series began and ended with 30 s of static stimuli. Subjects were instructed to focus their attention on the stimuli. Participants were asked to fixate the central cross during the visual task and to keep their eyes closed while performing the tactile task. Sensory modality (tactile or visual) and hand of stimulation (left or right) were constant for each time series. Tactile right hand, tactile left hand, and visual time series were presented in a pseudorandom sequence counterbalanced across subjects.

Image Analysis

We used the AFNI package to analyze functional imaging data (<http://afni.nimh.nih.gov/afni>, Cox 1996). All volumes were registered to the volume collected nearest in time to the acquisition of the high-resolution anatomical scan using the program 3dvolreg. Slice acquisition times were aligned using 3dTshift. Images were smoothed spatially (isotropic Gaussian filter, $\sigma = 3.4$ mm). Statistical analysis was performed using multiple regression to identify regions significantly involved in the perception of tactile and visual motion. For the tactile and visual conditions, the mean response to each moving stimulus was modeled with a separate regressor, obtained by convolution of the task with a standard hemodynamic response model. The 6 movement parameters derived from the motion correction were included as regressors of no interest. The significance of the response to each type of stimulus motion was calculated using a general linear test that aggregated data across all regressors for a type of motion. Individual Z maps for each of the contrasts of interest were transformed into the standard Talairach and Tournoux atlas (Talairach and Tournoux 1988) coordinate system and resampled to 1 mm³ voxels. Group Z maps were computed by multiplying the cross-subject average Z values by the square root of

the sample size. Activations were anatomically localized on the sighted and blind group-averaged Talairach-transformed T_1 -weighted images. Significant response during tactile or visual flow perception was defined by a Z threshold of 3.48 ($P < 0.0005$).

Results

Optic flow perception evoked robust bilateral activation in lateral occipital and posterior inferior temporal cortices, including the location of hMT+ and of other motion-responsive visual areas, such as V3A and V7, in both sighted and congenitally blind subjects (Table 1). In sighted subjects, tactile flow perception also evoked bilateral activation in the anterior part of the inferior temporal region activated by optic flow (Fig. 2). Perception of tactile flow deactivated a region (Talairach coordinates: $x = 44$, $y = -70$, $z = -4$) in the more posterior part of the area activated by optic flow in the right hemisphere. With a more liberal threshold (Z score > 2 , Fig. 3), a similar deactivation was seen also in the left hemisphere (Talairach coordinates: $x = -46$, $y = -77$, $z = 2$), and additional peaks of significant deactivation can be seen in the right hemisphere (Talairach coordinates: $x = 44$, $y = -74$, $z = 4$; $x = 41$, $y = -75$, $z = -5$). A negative response in the dorsal occipital cortex in the sighted subjects is also near the coordinates of V3A/V7 (Table 1). In blind subjects, tactile flow also evoked bilateral activation in the lateral occipital and posterior inferior temporal cortices. The activation of this region during tactile flow perception was greater in spatial extent in the blind subjects as compared with the sighted subjects (4.1 vs. 0.7 cc for blind and sighted subjects, respectively, $P < 0.005$) and included the more posterior part of the region that was activated by optic flow but deactivated by tactile flow in the sighted subjects (Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>).

In addition to the lateral occipital and inferior temporal cortical areas, optic and tactile flows both evoked activations in the intraparietal sulcus bilaterally and in a more ventral and anterior inferior temporal region that responds during both tactile and visual object recognition (Amedi et al. 2001; Pietrini et al. 2004). As expected, modality-specific visual and tactile sensory regions were also activated during the visual and tactile tasks, respectively (for a complete list of activated regions, see Table 1).

Perception of translational and rotational optic flows evoked maximal responses in different parts of the hMT+ complex, bilaterally, with a more dorsal location for translational flow and a more inferior location for rotational flow (Fig. 4). This result replicates the finding of Morrone et al. (2000). By contrast, perception of translational and rotational tactile flows in both sighted and blind subjects did not evoke distinct peaks of response analogous to those found for visual flow.

Discussion

This study was designed to investigate the role of the visual area hMT+ in the perception of tactile flow. We compared the activation of this area during tactile flow perception in sighted subjects and in individuals with congenital or early blindness to assess the role of visual imagery in the representation of tactile flow and the role of visual experience in the development of the functional organization of this area. The results showed that tactile flow perception in sighted subjects activated an anterior part of the lateral occipital and inferior temporal cortical areas that responded to visual flow but deactivated a more posterior part of that complex. Tactile flow perception in blind subjects activated a more extensive region in the lateral occipital and

inferior temporal cortical areas that included the more posterior part that was activated by visual flow and deactivated by tactile flow in the sighted subjects. These findings indicate that visual imagery is not necessary for the involvement of hMT+ in the representation of tactile flow. Furthermore, visual experience is not a necessary prerequisite for the development of a functional architecture in hMT+ that plays a more general role in processing sensory flow. Interestingly, visual experience appears to lead to a segregation of the motion-responsive lateral occipital and inferior temporal cortices into subregions: a more anterior part that is involved in the representation of both optic and tactile flows and a more posterior part that is involved only in the representation of optic flow. Tactile flow perception in sighted subjects deactivated the posterior part. If the functional development of these cortical regions proceeds in the absence of visual experience, the entire structure is involved in the representation of tactile flow. These results suggest that competitive interactions between visual and tactile inputs in normal development lead to functional specialization in motion-responsive cortex that does not develop in the absence of visual input.

Others have shown that the perception of tactile motion elicits neural activity in the hMT+ complex (Hagen et al. 2002; Blake et al. 2004). These studies examined the response in an hMT+ region of interest defined by response to visual motion and, consequently, did not address whether the distribution of activity elicited by tactile motion differed from the distribution of activity elicited by visual motion. The study by Blake et al. (2004) also showed that tactile perception of flow interacted psychophysically with visual perception by disambiguating the direction of rotation of a visually transparent sphere.

A relatively high intersubject variability in the anatomical characterization of visual motion-responsive subregions is present across functional and structural brain imaging studies. Specifically, with current blood oxygenation level-dependent methodology at 1.5 T, the functional definition of the contiguous subregions of hMT+ the lateral occipital complex (LOC), and LOTv poses some difficulty (Smith et al. 2006). Furthermore, the ventral part of MT+ and the dorsal part of LOC may even share an overlapping subregion that is involved in both visual motion and object recognition (Kourtzi et al. 2002). We cannot rule out that the areas of deactivation shown by sighted subjects during perception of tactile flow are on the border between MT+ and the dorsal portion of LOC. Moreover, by using a more liberal threshold (Z score > 2 ; $P < 0.05$), we found a similar area of deactivation in the left hemisphere (Talairach coordinates: $x = -46$, $y = -77$, $z = 2$) and additional peaks of deactivation in the right hemisphere (Talairach coordinates: $x = 44$, $y = -74$, $z = 4$; $x = 41$, $y = -75$, $z = -5$), indicating that the peaks of deactivation during tactile flow in the 2 hemispheres overlap with the coordinates of the visual MT+ area.

Previous studies have demonstrated functional distinctions between regions of the hMT+ complex that presumably correspond to areas MT and MST in the brain of the macaque monkey. Our results replicated the difference between peaks of activation for perception of translational and rotational optic flows that was reported by Morrone et al. (2000). Interestingly, this distinction was not observed for the neural responses in either sighted or blind subjects during perception of translational and rotational tactile flows. Whereas visual perception allows for parallel processing of a large sensory field, the more spatially focused perception of tactile flow, especially when using only the index and middle fingers of one hand as in our

Table 1

Z scores and Talairach atlas coordinates for the different local Z score maxima (cluster size >150 μ L and local maxima distance >20 mm) in those regions that responded significantly ($P < 0.0005$) during optic and tactile flow perception in sighted and blind subjects

Brain areas	Hemisphere	Sighted								Blind			
		Tactile flow				Optic flow				Tactile flow			
		Z	x	y	z	Z	x	y	z	Z	x	y	z
Ventral occipital hMT+	R	5.3	44	-48	-5	9.7	43	-73	7	5.1	38	-67	10
	L	4.7	-49	-62	5	9.1	-46	-62	7	5.0	-45	-79	9
LOC/LOtv	R	-4.4	44	-70	-4								
	R					3.6	47	-47	-17	5.9	37	-54	-6
V1/V2	R					5.4	51	-55	3				
	L					5.8	-55	-50	-10	7.1	-51	-64	-5
	R					5.1	15	-90	8	5.0	0	-89	3
	R					4.4	19	-76	-14				
V4	R									3.6	37	-85	1
	L					4.4	-11	-80	-3				
Dorsal occipital V3A	R	-4.4	-32	-79	-15								
	L					7.8	25	-81	25	5.4	8	-94	23
V7	R	-4.5	39	-73	29	7.8	-28	-81	21				
	L	-4.5	-41	-59	22								
Superior frontal	R	-4.4	9	55	32					4.2	32	45	31
	R									4.1	36	46	26
	R					-4.9	21	56	7				
	R					-3.9	22	20	40				
Anterior frontal	L					4.5	-17	15	62	4.6	-32	59	22
	R	-4.7	25	54	9								
Medial/orbitofrontal	R	-3.9	-19	-44	-48								
	L					-4.5	0	55	19				
Middle frontal	R					-4.4	-30	46	-5				
	R	8.6	50	5	36	4.7	45	7	28	5.5	59	14	21
	L	7.2	-55	1	36	5.7	-48	3	44	6.1	-53	10	30
Anterior cingulate	L	-4.3	-33	11	47								
	R					-5.0	3	34	39				
Inferior frontal/insula	L					-4.5	-7	48	0				
	R	7.5	56	9	7					4.5	54	1	7
	R	5.5	41	-1	16								
	L	6.7	-57	7	13								
Insula/anterior temporal	R					-4.5	-24	25	-12				
	L					-4.2	39	-13	9				
Precentral	R	-4.8	-51	-17	-6								
	L	10.0	30	-9	63	5.4	21	-6	64	5.4	38	-7	55
Supplementary motor	R									-5.9	14	-23	74
	R					6.5	-27	-3	60	6.6	-40	-7	54
	L									-3.7	-19	-17	73
	L									5.6	4	4	48
Primary sensorimotor	R	4.1	3	7	63								
	L	7.0	-7	-10	68	-4.5	-2	-9	57				
	R	14.3	44	-29	49	4.7	51	-29	44	9.8	47	-24	47
	L	-4.8	15	-29	61					8.8	37	-37	60
Secondary sensorimotor	R	15.0	-43	-28	54	4.6	-51	-20	46	11.6	-57	-19	36
	L	5.8	-26	-38	69	-4.4	-13	-31	54	10.4	-42	-37	60
	R									-4.6	-11	-36	69
	R	13.8	55	-20	21					3.6	41	-11	17
Posterior parietal and intraparietal sulci	R									6.7	61	-15	34
	R									4.1	41	-37	28
	L									5.4	-35	-36	-26
	L	10.7	-57	-17	23					6.8	-49	-8	18
Posterior parietal and intraparietal sulci	R	4.8	-52	-37	22					5.3	-50	-34	23
	R					11.2	23	-57	61	5.4	56	-48	38
	R					6.3	27	-39	42				
	R					7.0	19	-70	44	5.7	4	-77	34
Precuneus	R									4.6	5	-48	72
	R					3.7	0	-56	58	5.2	23	-72	52
	L									4.8	42	-58	52
	L					9.2	-23	-58	57	6.2	-32	-57	57
Parahippocampal gyrus/amygdala	R	-5.1	-9	-53	63	5.8	-38	-40	55	3.9	-56	-47	42
	L	-3.7	-19	-44	48	4.3	-24	-70	41	6.2	-21	-77	42
	R					-3.7	6	-50	36				
	L					-4.8	-7	-63	28				
Posterior cingulate/parahippocampal gyrus	R	-4.2	-9	-74	49								
	L	-4.1	-30	-77	36								
	R	-5.0	19	-18	-21								
	L	-4.0	-20	-19	-22								
Cerebellum	R	-6.0	1	-45	35	-4.0	7	-56	15				
	L	-3.7	-8	-53	18	-4.1	-11	-44	5				
	R	8.8	19	-61	-15					4.5	18	-52	-21
	R	3.9	22	-35	-21					5.3	36	-65	-23
Basal ganglia	R									3.9	4	-73	-22
	R									4.2	31	-44	-35
	L	7.0	-25	-50	-17	6.3	-26	-60	-15				
	L	3.9	-5	-69	-10	5.2	-32	-84	-9				
Basal ganglia	L	5.5	-20	-53	-38	4.0	-1	-66	-22				
	R									4.6	18	-15	-7

Note: A possible functional labeling with visual subregion mapping is suggested for ventral and dorsal occipital areas.

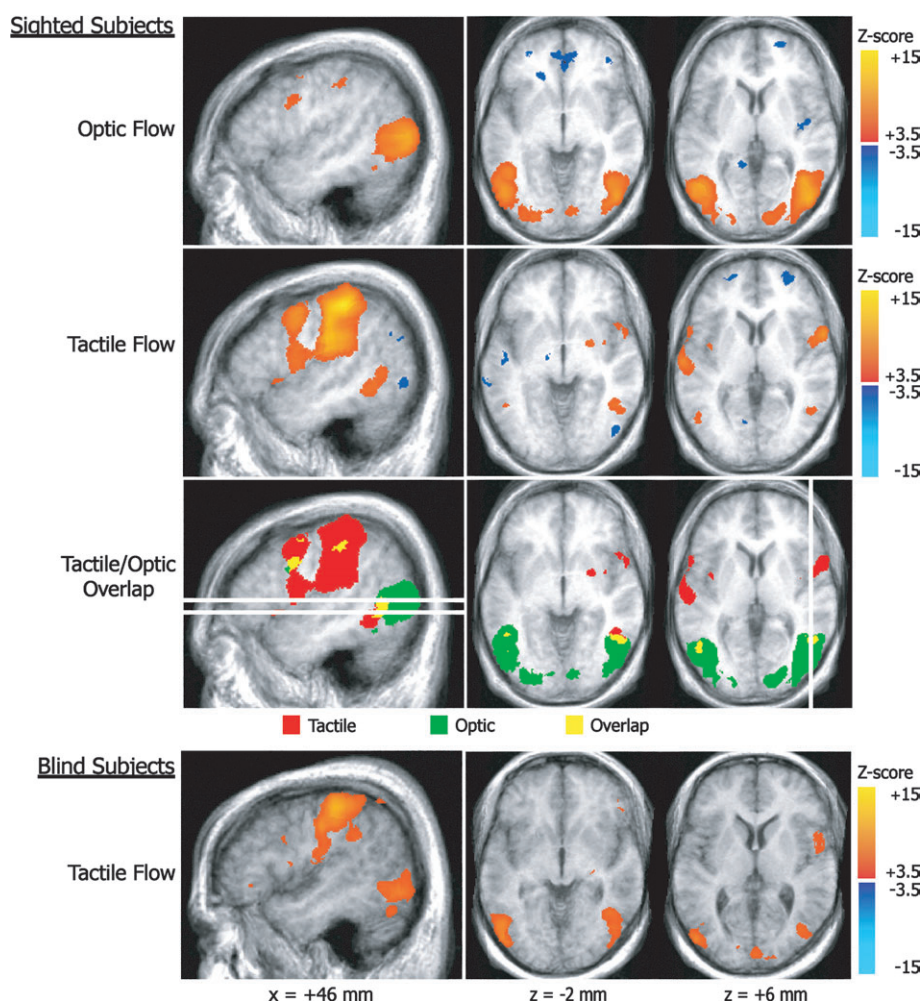


Figure 2. Brain areas that responded during tactile or optic flow perception in sighted subjects and during tactile flow perception in blind subjects. Sagittal and axial images from group Z score maps of activated areas are shown for the sighted and blind subjects. The tactile/visual overlap map shows the areas activated by both tactile and optic flow perception (shown in yellow), as well as the areas activated only by tactile (red) and optic (green) perception. The white lines in the sagittal image correspond to the locations of the axial slices, and similarly, the white line in the axial slice indicates the location of the sagittal section.

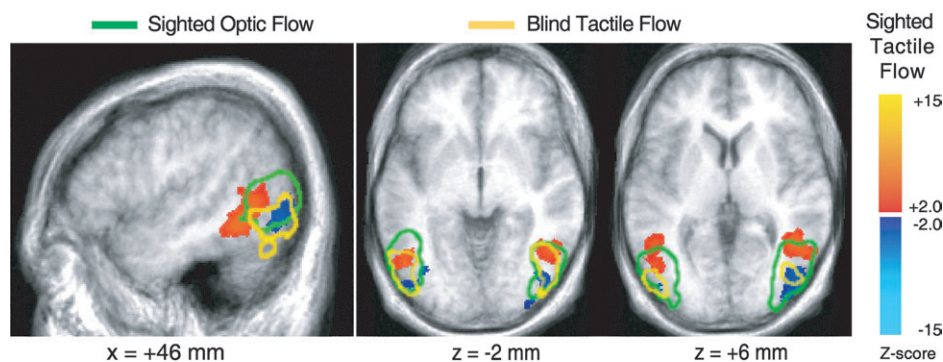


Figure 3. Areas within or near visually defined hMT+ that were activated and deactivated during tactile flow perception in sighted subjects are shown in red (activation) and blue (deactivation). These areas are shown relative to the regions that were active during optic flow perception in sighted subjects (green outline) and tactile flow perception in blind subjects (yellow outline). The threshold for showing these colored regions was lowered to $P < 0.05$ to illustrate that the deactivation in posterior hMT+ showed a trend to bilaterality, even though only the right side was significant when using our stricter threshold ($P < 0.0005$).

experiment, may prevent the formation of a more global representation of translational and rotational movements.

Sensory flow plays an essential role in the perception of objects and in the perception of one's movement relative to

external objects and the environment. Representation of sensory flow is integrated with the representation of limb and body movement to disambiguate self-motion from object motion. The input for perception of flow can be visual, tactile,

Sighted Optic Flow

- Translation
- Rotation
- Overlap

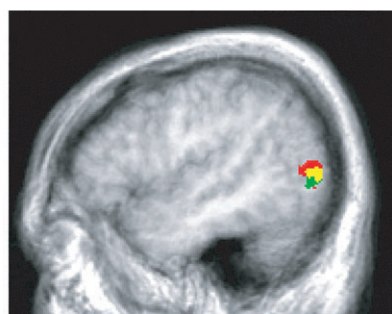


Figure 4. Areas in hMT+ that were differentially activated by perception of translational and rotational optic flows, shown on a right sagittal image ($P < 10^{-8}$). The overlap map shows the area activated only by translational flow (red), only by rotational flow (green), and by both translational and rotational optic flows (yellow).

or auditory. Even olfactory flow likely plays an important role for goal-directed locomotion, probably more so for nonhuman animals. Our results show that tactile and optic flows elicit activity in overlapping brain areas, suggesting that they may share a common, or at least closely related, neural representation that may be based on similar neural computations. Indeed, tactile and visual flows can be modeled with the same computations and show similar psychophysical illusions (Bicchi et al. 2003).

However, compared with visual presentation of optic flow, tactile stimulation shows several differences. For instance, whereas visual perception allows for the simultaneous processing of a large sensory field, perception of tactile flow is necessarily more spatially limited. This may impede the formation of a more global representation of movements and contribute to the difference in the responses in hMT+ for the 2 sensory modalities. Moreover, one could argue that tactile perception of flow may involve more attentional resources than visual perception because of its novelty for the subjects, resulting in differential activation in hMT+. However, we attempted to minimize the effect of novelty by having subjects undergo a training session prior to magnetic resonance scanning, during which they were familiarized with both the visual and tactile flow stimulations.

We and others have shown that supramodal representation exists in other visual extrastriate cortical areas for other types of information that can be gleaned from visual and tactile stimuli. Object recognition by sight or touch evokes neural activity in the inferior temporal region LOTv (Amedi et al. 2001, 2002, 2005; James et al. 2002; Stoesz et al. 2003; Pietrini et al. 2004; Prather et al. 2004; Reed et al. 2005). Spatial working memory and mental rotation for visual or tactile stimuli evoke neural activity in posterior parietal cortex (Prather et al. 2004; Reed et al. 2005; Zhang et al. 2005; Ricciardi et al. 2006). These results suggest that information that is represented in visual areas about sensory flow, object form, and spatial relationships does not have to be necessarily visual in nature. These representations can be activated by nonvisual sensory input, do not depend on visual imagery, and can develop with no history of visual experience. Their location in visual cortex may reflect the dominance of vision for obtaining this type of information from the sensory environment (Amedi et al. 2005). The supramodal nature of these representations may underlie the ability of congenitally blind individuals to acquire normal knowledge of the world and interact effectively with their environment (Pietrini et al. 2004).

Supplementary Material

Supplementary material can be found at <http://www.cercor.oxfordjournals.org/>.

Notes

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